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KAIRA IS A LIKELY SISTER GROUP TO *METEPEIRA*, AND *ZYGIELLA* IS AN ARANEID (ARANEAE, ARANEIDAE): EVIDENCE FROM MITOCHONDRIAL DNA

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ABSTRACT. Various authors have offered three alternative hypotheses of phylogeny which suggest different sister groups to the orb-weaving spider genus *Metepeira*. In one case *Kaira* is sister genus to *Metepeira*, and *Zygiella* is sister to *Kaira* plus *Metepeira*; in another case, *Kaira* is sister genus to *Metepeira*, but *Zygiella* is a tetragnathid, and thus unrelated at this level of analysis; and in the last case, *Zygiella* is close to *Metepeira*, but this time *Kaira* is not closely related. To resolve among these conflicting hypotheses, six species of orb-weaving spiders were sequenced for mitochondrial DNA encoding a portion of the 12S ribosomal subunit. These data were analyzed with data from two tetragnathid orb-weavers to estimate the phylogenetic relationships among these spiders and to determine which genus is a likely sister group to *Metepeira*. Phylogenetic analysis using parsimony supports the hypothesis that *Kaira* is a likely sister group to *Metepeira* and that *Zygiella* is in the family Araneidae rather than the family Tetragnathidae.

Relationships among orb-weaving spiders are, in general, poorly understood (Coddington & Levi 1991). In particular, it is not known which genus within the araneids is most closely related to the genus *Metepeira* F.P.-Cambridge 1903. Such information is valuable to a phylogenetic analysis of *Metepeira* (about 40) species because it uncovers ancestral character states and shows patterns of character evolution among species (Maddison et al. 1984). It is our intention in this paper to compare 12S mtDNA sequences of several selected taxa in order to determine which among them is the closest outgroup to *Metepeira*.

Scharff & Coddington (in press) hypothesize that *Kaira* O.P.-Cambridge 1889 and *Metepeira* are sister groups because both genera share the loss of the stipes and have a median apophysis with a pair of prongs and a toothed anterior margin (compare fig. 82 with fig. 127 in Levi 1977). Thus, we targeted *Kaira* as a potential sister group to *Metepeira*. Somewhat similar median apophyses are also found in *Aculepeira* Chamberlin & Ivie 1942 and *Amazonepeira* Levi 1989, but that of *Kaira* is the most similar. Genitalic and somatic characters in *Amazonepeira* and *Aculepeira* align them closer to *Araneus* Clerck 1757 rather than to *Metepeira* (Levi 1977, 1989, 1993).

Simon (1895), who was one of the first arachnologists to discuss relationships among orb-weaving spiders in detail, did not consider *Kaira* and *Metepeira* to be closely related. His classification created four sub-families within what he called the Argiopidae (= Araneoidea), including Argiopinae (= Araneidae), which contained 28 "groups", two of which were Poltyeae and Araneae. The Poltyeae group contained *Kaira*; the Araneae group consisted of four "series", largely defined by eye arrangements. Many species which today are called *Araneus*, as well as some species affiliated to *Larinioides* Caporiacco 1934, were placed in series number 2. *Metepeira* and *Zygiella* F.O. Pickard-Cambridge 1902 were placed in series number 3. (Fig. 1, right column).

Zygiella is another genus which we have targeted as a candidate sister group to *Metepeira*. Scharff & Coddington (in press) agree with Simon that *Zygiella* is close to *Metepeira* based on their morphological cladistic analysis. Coddington (1990) suggests that *Zygiella*, which has a radix, distal hematodocha, and terminal apophysis, belongs to the Araneidae (Fig. 1, middle column) and not the Tetragnathidae. This placement is in keeping with three synapomorphies that are thought to unite the Tetragnathidae, yet are absent in *Zygiella*:

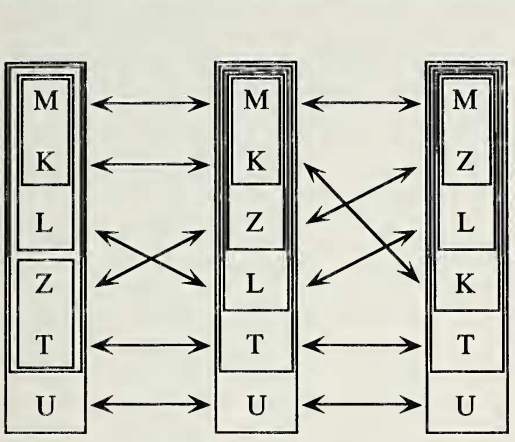

Figure 1.—Schematic diagrams illustrating three hypotheses of relationships for six orb-weaving taxa; hierarchical relationships are depicted as nested sets of Venn diagrams. Left column, hypothesis of Levi (1977, 1980); middle column, hypothesis of Scharff & Coddington (in press); right column, hypothesis of Simon (1895). Abbreviations: M, *Metepeira*; K, *Kaira*; Z, *Zygiella*; L, *Larinioides*; T, *Tetragnatha*; U, *Uloborus*.

apical tegular sclerites, loss of the median apophysis, and a conductor that wraps a free embolus (Hormiga et al. 1995). In contrast, Levi (1980) considers *Zygiella* and *Metepeira* not to be closely related. He placed the former in the Metine group of the Tetragnathidae based on the closely spaced eyes and the conical tibia (Fig. 1, left column).

To help decide among the hypotheses of Levi (Fig. 1, left column), Coddington & Scharff (Fig. 1, middle column), and Simon (Fig. 1, right column), we sequenced 12S ribosomal mtDNA from two individuals representing different species of *Metepeira*, and one individual from each of *Kaira*, *Zygiella*, *Larinioides*, and *Uloborus* Latreille 1809. These sequences were analyzed with Gillespie et al.'s (1994) data for *Tetragnatha* Latreille 1804 and *Doryonychus* Simon 1900 (family Tetragnathidae). Obviously, these eight taxa form an extremely limited sample, but the intention here is to help us select among the three main taxonomic hypotheses relating to *Metepeira* rather than to attempt a comprehensive analysis of the Araneidae.

METHODS

The six female spiders chosen for mtDNA extraction, amplification, and sequencing were: *Metepeira daytona* Chamberlin & Ivie 1942, from Flagler Beach, Florida (29°37′N, 82°23′W); *Metepeira minima* Gertsch 1936, from Tamaulipas, Mexico (22°30′N, 99°4′W); *Kaira alba* (Hentz 1850), from Lake Lochloosa, Florida (29°37′N, 82°23′W); *Zygiella atrica* (C.L. Koch 1843), from Nahant, Massachusetts (42°25′38.7″N, 70°56′9.1″W); *Larinioides sclopetaria* (Clerck 1757), from Cambridge, Massachusetts (42°20′N, 71°6′W); and *Uloborus glomosus* Walckenaer 1842, from Sherman, Connecticut (41°34′30″N, 73°31′16″W). Specimens were collected in 80% or 100% ethanol. Vouchers were deposited at the Museum of Comparative Zoology.

Tissue for extraction was dissected primarily from the prosoma: the carapace was lifted away, tissues were removed, and in many cases the carapace replaced so that the specimen appeared unaltered. For some smaller specimens, muscle fibers were also taken from the chelicerae and femora. Care was taken to exclude the cuticle which, if present, could hinder amplification (J.K. Wetterer pers. comm.).

Using chilled glass homogenizers, tissues were ground twice in 100 µl of 50 mM Tris-Cl, 20 mM EDTA, and 2% SDS. To digest the proteins, the extractions were incubated with 2 µl of 100 ng/ml proteinase K in a 60 °C oven for 1 h. To remove cell walls and residual ionic compounds, 100 µl of saturated NaCl were added. The extractions were cooled on ice for 30–70 min and then centrifuged for 15 min at 4 °C. The supernatant was retained and the DNA was precipitated with 100% EtOH, washed with 70% EtOH, dried in a centrifuge under vacuum, and resuspended in 100 µl 1xTE (10mM Tris-HCl and 1 mM EDTA).

A 257 bp region of the third domain of the 12S ribosomal subunit was amplified and sequenced for most taxa using primers 12St-L and 12Sbi-H (Croom et al. 1991). Mitochondrial DNA from *U. glomosus* failed to work with 12St-L, so 12S-U [a degenerate arthropod-specific primer designed by D. Fitzpatrick (5′-TGTTT(AT)(AGT)TAATCGA(ATC)(AT)(ACT)T(AC)CACG-3′)] was used instead. Two µl of template were used in 100 µl PCR reactions (50 mM KCl; 10 mM Tris-HCl; 0.1% Triton® X-100; 2.5 mM $MgCl_2$; 0.5 µM of each primer; 2.5 units of Taq; and 0.2 mM dNTP) and cycled 30–35 times (45 sec at 94

Table 1.—Genetic distances among different species of orb-weavers. For each pairwise comparison, corrected percent distances [based on the Kimura two-parameter model (Li et al. 1985) and generated by Heap Big (Palumbi, unpub. program)] appear above the diagonal, percent transversions below the diagonal. Column headings, *M. day = Metepeira daytona, M. min = Metepeira minima, K. alb = Kaira alba, Z. atr = Zygiella atrica, L. scl = Larinioides sclopetaria, U. glo = Uloborus glomosus, D. rap = Doryonychus raptor, T. per = Tetragnatha perreira.*

	M. day	*M. min*	*K. alb*	*Z. atr*	*L. scl*	*U. glo*	*D. rap*	*T. per*
M. daytona	—	13	18	31	30	45	49	44
M. minima	3	—	21	35	28	45	57	48
K. alba	9	7	—	27	25	44	53	41
Z. atrica	18	18	18	—	25	39	49	32
L. sclopetaria	17	14	16	17	—	44	39	36
U. glomosus	24	23	27	24	27	—	43	42
D. raptor	27	27	28	26	25	24	—	28
T. perreira	23	23	23	18	22	26	16	—

°C; 60 sec at 42 °C; 90 sec at 72 °C). The PCR products were purified on a low melt agarose gel: bands corresponding to DNA of the appropriate length were cut from the gel, and DNA was isolated from the agarose using phenol or spin columns (QIAquick, by QIAGEN®). The PCR product was sequenced in both directions using DyeDeoxy™ termination (Perkin-Elmer Kit) with the same primers used in amplification. Sequence products were purified with CENTRI-SEP columns (Princeton Separations, Inc.) and then run on a ABI 370A autosequencer (Applied Biosystems, Inc.). Chromatogram sequence data generated by the autosequencer were edited by eye using SeqED (Applied Biosystems, Inc.).

Sequence data collected by Gillespie et al. (1994) using the same primers on two Hawaiian tetragnathid species, *Tetragnatha perreira* Gillespie 1991 from Oahu and *Doryonychus raptor* Simon 1900 from Kauai, were added to our data set and aligned using Clustal V (Higgins et al. 1992). The resulting alignment was further adjusted by hand and cropped to form a character matrix using SeqApp (Gilbert 1994). Corrected pairwise percent distances based on the Kimura two-parameter model (Li et al. 1985) were calculated using the program Heap Big (Palumbi unpub. program). An exhaustive search for the most parsimonious tree and bootstrap analysis were performed using PAUP (Swofford 1991) on sequence characters for all eight species, holding *U. glomosus* as the outgroup. Trees were compared and manipulated with MacClade (Maddison & Maddison 1992).

RESULTS

The resulting character matrix is 208 bases long (Fig. 2). An exhaustive search using PAUP (Swofford 1991) yields two most parsimonious trees, each 227 steps long, C.I. with all characters, 0.75; C.I. with uninformative characters excluded, 0.67; and R.I. of 0.54. The two trees disagree only in whether *L. sclopetaria* is more closely related to *K. alba* plus *Metepeira* or whether it is more closely related to *Z. atrica*. The strict consensus of these two trees is illustrated in Fig. 4. Although pairwise genetic distances (Table 1) are quite high, skewness test statistic (g_1) calculated by PAUP is -0.81, which is statistically significant ($P < 0.01$), indicating that there is, nonetheless, strong phylogenetic signal (Hillis & Huelsenbeck 1992). Furthermore, an exhaustive search with *U. glomosus* excluded results in a single most parsimonious tree with *Z. atrica* most closely related to *Metepeira* plus *K. alba*—a result that is still compatible with Fig. 4.

Of the 76 unambiguous changes on the tree (i.e., character state changes that optimize to a single, specific branch segment), 31 are transitions (purine to purine or pyrimidine to pyrimidine) and 45 are transversions (purine to pyrimidine or pyrimidine to purine). This paradoxically low ratio of transition to transversion events increases with decreasing branch lengths (Fig. 3) and therefore is evidence for multiple hits and saturation between distant relatives (Simon et al. 1994). However, a transition to transversion ratio of 0.69 is still with-

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                                    .10        .20        .30        .40
Metepeira daytona                   TACTCTTATTTAAA-TCTTATATACCTCCATCTTAAGAATTAATATCTA
Metepeira minima                    ....T.........-..................C...G...........
Kaira alba                          C...T.........A.T.....................T...G..A-A.
Zygiella atrica                     C...TA..AC....-.............................-AT
Larinioides sclopetaria             ....T.........-.............................A-AT
Uloborus glomosus                   C...T.A.A.....AGT.........G....AA..-.....T-.C.TC.
Doryonychus raptor                  ....TGG.....T.-.T.......T....G.A-.C-....AT..C.-A.
Tetragnatha perreira                C...T...A...T.-.T.........G..G..-.T-....AG..T.-A.

.50        .60        .70        .80        .90        .100       .110       .120
TATTCTCTTCTAAACAGAAATTC--TAAAAAGTTAGGTAAAGGTGTAGACTACATAAGAGTTTATGTGGGTTACAATAAA
.......CC.CT..T.........--...G.............................A..C.GGG...............
C..A..A....C..A.T.....TTT...C.....................C.T....A......G...............
A.A.-.T.-T.C..A.T....AT-T...T.....................TT..TA..A..TGA..T......T.....
ATA.T.T.-T.CTTA.T..T..T-T...T.T...................A.T....A..A.A.GA...A.....T.....
A...AC-AAT.C..A.T..TA.T-A......TA.....C.........ATT..A..TTA..AGAGGA..T......T.....
ATA.A.-.AT.C.CA.T..TA.T-A......T.....................CCA....A.AA..TA.....T.....
A.A.T.-.AT.C..A.A...A.T-C......T.............A....TT...A..ACA.AA..TA.....T.....

.130       .140       .150       .160       .170       .180       .190       .200
TTCTATTTAAGAATATATAATTAAAATTTTAT-TTGAAAAAGGATTTGTAAGTAAAT-TAAAAATAATATTCTTTATTG
.CT........?....T.............A-.............A.......T.-...G..........C...A..
..A.......AG....TA.........A..T.-C.....G.......A.......T.-...........A.T....A..
..AG.......G.A..TA.T.A....A..A..-AA....G.......AACT......-.T...C..T....T.AA....
..T.......AG..T.T.T......TA.AA..-.............A.T.....T.T.TTT....T....TAA..A..
A.TA.......G...AT...A.TTT.A....AT..T...........AAT.T.....-AT...T-..A.A.T.A.....
AA.A.......GC.TA..GTA....TCGCAT.-A.A....C......A......T.A-.TTTTT...A.AAAAAGT...
.AAA.......G..CG.GTTAA.T.TAA..TC-AA...........A......TTA-.TT..T.......AAAAT...
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Figure 2.—Matrix of 208 characters from aligned 12S ribosomal mtDNA sequences. Data for eight orb-weaving taxa are represented, two of which (*Doryonychus raptor* and *Tetragnatha perreira*) were published in Gillespie et al. (1994).

in the range of other comparable and successful phylogenetic analyses, such as 0.61 for the analysis of tetragnathid relationships by Gillespie et al. (1994).

DISCUSSION

Our data support the Scharff and Coddington hypothesis (compare Fig. 4 with Fig. 1, middle column) and thus provide evidence that *Kaira* is, indeed, a likely sister-group to *Metepeira*. Despite the fact that *Metepeira* is a morphologically homogeneous taxon with a restricted distribution, thus presumably with a relatively recent inception, the within-*Metepeira* distances are not much shorter than those between *Metepeira* and *Kaira* (Table 1). Furthermore, the *Kaira-Metepeira* clade is supported by 94% of 1000 bootstrap replicates and eight unambiguous apomorphies (Fig. 4).

Nonetheless, the branch lengths between clades seem more evenly spaced than what one might at first expect, given that some unite closely related taxa, whereas others unite distantly related taxa. However, this may merely reflect multiple substitutions, in which long genetic distances are vastly underestimated when new mutations occur at the same sites as the old mutations. Evidence for this occurrence can be seen in the attenuation of

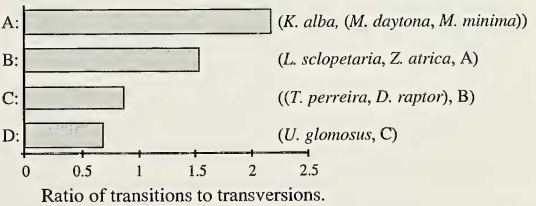

Figure 3.—Ratio of unambiguous transitions to unambiguous transversions for increasingly inclusive clades as calculated by MacClade (Maddison & Maddison 1992). Clade A includes *Kaira alba*, *Metepeira daytona*, and *M. minima*; clade B includes *Larinioides sclopetaria*, *Zygiella atrica*, and clade A; clade C includes *Tetragnatha perreira*, *Doryonychus raptor*, and clade B; clade D includes *Uloborus glomosus* and clade C.

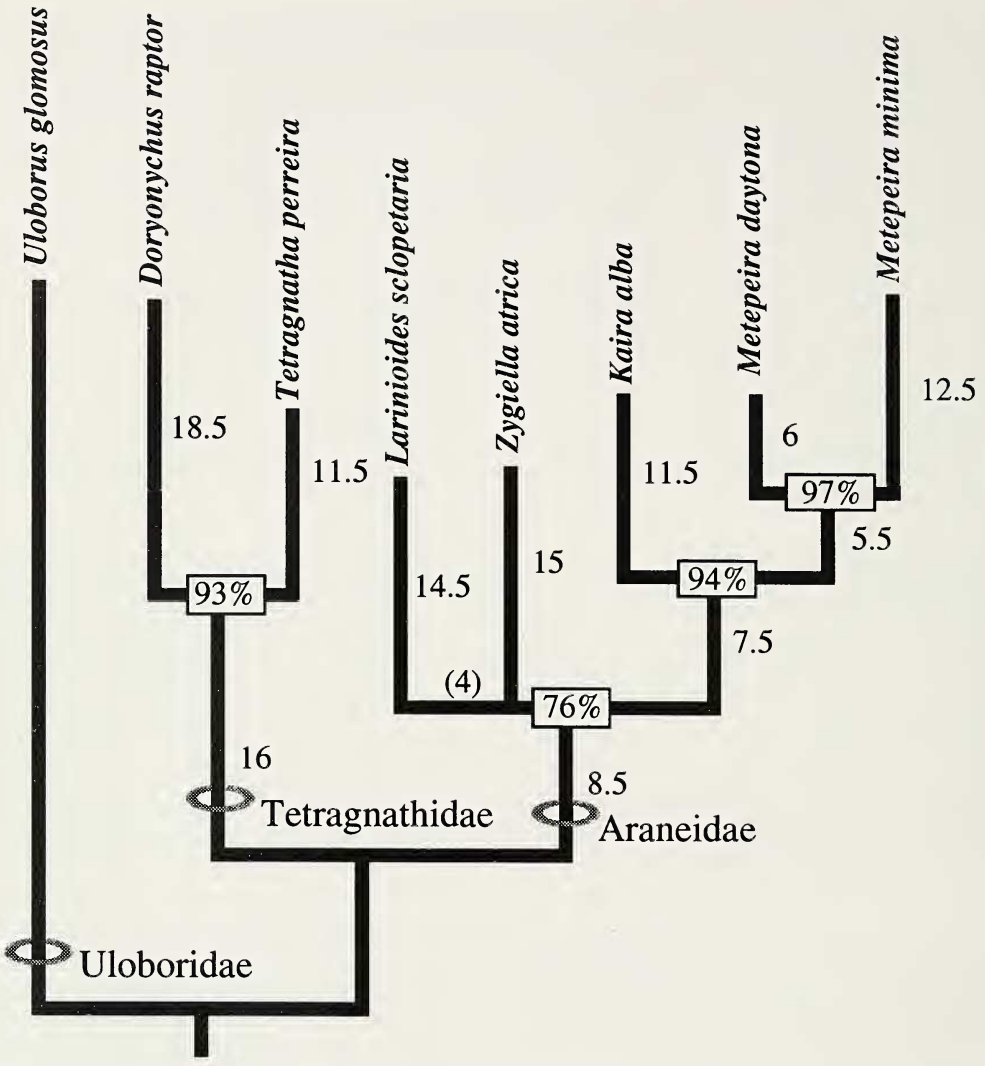

Figure 4.—Strict consensus tree of the two most parsimonious phylogenetic trees from 208 bases of the 12S ribosomal mtDNA subunit (tree length = 223+ steps; C.I. using all characters = 0.79; C.I. using informative characters only = 0.75). Figures adjacent to each branch indicate the number of unambiguous character changes averaged between the two most parsimonious trees. The figure in parentheses indicates the number of unambiguous character changes between where *L. sclopetaria* or *Z. atrica* branch from the main stem in either shortest tree. Percentages are bootstrap values for each node from 1000 replicates.

the transition to transversion ratio when measured over increasingly inclusive clades (Fig. 3). Although transitions occur more frequently than transversions, accumulation of transversions in older, longer branches will mask the activity of transitions (Simon et al. 1994). The pronounced attenuation of the transition to transversion ratio in our data suggest that the *Kaira* is actually closer to *Metepeira*, yet farther from the other taxa, than what the tree would appear to show. The same can be said for the separation between the araneids and the tetragnathids.

The close relationship between *Kaira* and *Metepeira*, as evidenced from our results, indicates that the shared flagellated median apophysis, as well as other genitalic characters, are likely to be homologous structures. Despite this particular similarity, *Kaira* and *Metepeira* share few other morphological features. *Kaira* has evolved numerous autapomorphies as a result of its highly specialized

predatory behavior. Convergent with *Mastophora* Holmberg 1876, *Kaira* has forgone orb-weaving, and is thought to emit pheromones that mimic those of female moths (Levi 1994; Stowe 1986). Thick, stubby setae on *Kaira*'s legs are presumably used to grab moths in flight, while a large array of tubercles on *Kaira*'s abdomen are thought to conceal or protect the exposed spider while it is in its hunting posture. In contrast, *Metepeira* has neither specialized leg setae nor abdominal tubercles, and it weaves a very distinctive web which combines orb and scaffolding with associated aerial retreat.

Identifying the sister group to *Metepeira* can help clarify phylogenetic structure and character evolution within the genus. Levi (1977) divided *Metepeira* species north of Mexico into two groups: *M. labyrinthea* and *M. foxi*. Species in the former group have a white line on a black sternum and a short keel on the median apophysis. Species in the latter group have a uniform sternum and a distal tuberculate keel on the median apophysis. Levi (1977) admitted that it "is difficult at present to decide which of these species groups is the derived and which the more primitive". Indeed, one needs an outgroup in order to determine which species group contains species arising basally and retaining symplesiomorphic characters, and which species group contains species arising more distally and sharing synapomorphic characters.

With *Kaira* as an outgroup to *Metepeira*, we can infer that the character states that define the *M. foxi* species group are primitive, and thus species in this group may arise basally within the genus *Metepeira*. Indeed, the distal tuberculate keel on the median apophysis is similar to modifications in the median apophysis of *Kaira* (compare figs. 82, 91–127 in Levi 1977). Furthermore, *Kaira* lacks the white line on a black sternum as seen in the *M. labyrinthea* species group. Also, within the *M. foxi* species group, *M. daytona* is probably the most basal species because the ratios between patella-tibia and metatarsus-tarsus articles are the same as they are in *Kaira* (about 1.1:1); whereas in all other known *Metepeira* species the ratio is about 0.9:1. Thus, with *Kaira* as the outgroup, our results support the relatively basal origins of species in the *M. foxi* species group. However, since this group is defined by exclusively symplesiomorphic characters, we cannot infer that it is monophyletic.

Nine unambiguous synapomorphies support the inclusion of *Z. atrica* within the Araneidae (Fig. 4). Forcing *Z. atrica* into the Tetragnathidae costs four additional steps. In addition, 1000 bootstrap replicates using PAUP support the araneid clade 76% of the time. Thus, our data disagree with Levi (1980) and others who believe that *Zygiella* is a tetragnathid.

However, we should mention that the monophyly of *Zygiella* is uncertain. On the one hand, the vacant sector in the orb web, the compact eye region, and the dorsoventrally flattened oval abdomen with its characteristic markings, seem to unite *Zygiella* species (Levi 1974). On the other hand, the inconsistency in the presence of a scape, terminal apophysis, paracymbium shape, tooth on the palpal endite, and seta on the palpal patella, put monophyly of the genus into question (Levy 1986). Levi (1974) argues that the remarkable diversity in *Zygiella* genitalia fails to break apart the genus because many inconsistent characters overlap one another. For example many species that lack a scape still share a derived ventral apophysis of the tegulum with other species that have a scape (Levi 1980). Thus, while it is still possible that *Zygiella* is paraphyletic, and while it is possible that some *Zygiella* species are, in fact, tetragnathids, our data argue that at least the type species for the genus, *Z. atrica*, appears to be an araneid.

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